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Diet, Feeding Behavior, Growth, and Numbers of a Population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia

Bruce C. Jayne

Harold K. Voris

Kiew Bong Heang

A Contribution in Celebration
of the Distinguished Scholarship of Robert F. Inger
on the Occasion of His Sixty-Fifth Birthday

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- MURRA, J. 1946. The historic tribes of Ecuador, pp. 785-821. In Steward, J. H., ed., *Handbook of South American Indians*. Vol. 2, *The Andean Civilizations*. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.
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Diet, Feeding Behavior, Growth, and Numbers of a Population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia

Abstract

Stomach contents were obtained from 181 of 611 *Cerberus rynchops* captured near the mouth of the Muar River in Malaysia. Of the prey items, 69% were the goby *Oxuderces dentatus*; however, as *C. rynchops* become larger, ariid catfish, mullet, and taenioid gobies are increasingly important portions of the diet. These species of prey, combined with direct observations, suggest that *C. rynchops* usually forage on or near the bottom or in very shallow water. Feeding behavior was observed for 23 *C. rynchops* which consumed 71 mudskippers. Initial seizure of the fish always involved marked lateral flexion of the neck. Snakes often held the fish before the initiation of swallowing, and regression analysis revealed holding was significantly longer with prey of larger size, which struggled more. The venom apparatus of *C. rynchops* is capable of immobilizing and killing fish smaller than 3 g. Recapture of 24 tagged snakes allowed estimation of average percentage of growth rates in snout-vent length (\bar{x} = 0.09%/day, range 0%–0.27%/day) and mass (\bar{x} = 0.36%/day, range –0.28%–1.43%/day). No evidence of a seasonal reproductive pattern was found. These aspects of the natural history of *C. rynchops* are compared to those of the sympatric species of marine snakes.

Introduction

The diverse assemblage of southeast Asian marine snakes includes three distinct taxonomic groups; homalopsines, acrochordids, and hydrophiids. *Cerberus rynchops* is one of several homalopsine species that is abundant in a variety of

coastal habitats (Wall, 1918; Smith, 1943; Gyi, 1970; Tweedie, 1983). Dunson and Minton (1978) found *C. rynchops* co-occurring with acrochordids and hydrophiids in mangrove areas of the Philippines. *Cerberus rynchops* can excrete salt via a salt gland (Dunson & Dunson, 1979) and can acquire some oxygen through cutaneous uptake (Heatwole & Seymour, 1978); however, these capacities apparently are not as well developed as those of the hydrophiids. Smith (1943) reported that *C. rynchops* is piscivorous, but the lack of data on the species of prey prevents determination of dietary overlap with sympatric species of marine snakes. *Cerberus rynchops* possesses opisthoglyphous dentition, but the role of this dentition in prey capture and manipulation is not known. The biological role of opisthoglyphous dentition is of considerable interest when discussing the evolution of ophidian venom apparatus (Kardong, 1980). *Cerberus rynchops* also has a relatively stout body and fragmented head scalation (Gyi, 1970), characters that Pough and Groves (1983) correlated with the proficient handling of large prey by snakes. However, the size of natural prey of *C. rynchops* has not been documented.

Most information on the natural history of marine snakes pertains to the hydrophiids. Dunson (1975) recently reviewed much of the literature and provided most information for Australian species. Much information about southeast Asian species has come from studies of the hydrophiids occurring in the main channel of the mouth of the Muar River in Johore, Malaysia. These reports have investigated diet (Voris & Voris, 1983), feeding behavior (Voris et al., 1978), reproduction, growth, and population size (Voris & Jayne, 1979; Lemen & Voris, 1981; Voris, 1985).

The purpose of this study is to expand the

knowledge of the marine snake fauna of the Muar River estuary by investigating several aspects of the natural history of *Cerberus rynchops* which occurs on the adjacent intertidal mud flat. First, the species composition and size of prey items are determined. Second, feeding behavior is analyzed, particularly to determine the role of opisthoglyphous venom apparatus and to quantify the effect of prey size on handling time. Third, growth rates and population size are estimated. Finally, comparisons are made with the sympatric species of marine snakes.

Materials and Methods

The fieldwork for this project extended from 14 January–5 March 1984 and 20 November 1985–8 February 1986. The primary site for this work was 400 m of shoreline along the south side of the mouth of the Muar River, Johore, Malaysia (fig. 1). Habitats at the shoreline include mud, sand, and gravel beach, man-made stone walls, and dense mangrove. From these varied shore habitats, the intertidal zone extends seaward as one continuous mud flat about 50 m wide at the mouth of the river to over 200 m wide at the mangrove area. A second site was 15 km southeast at the coastal fishing wharf of the town of Parit Jawa. This site was used for field observations of foraging behavior and as a supply of animals for the laboratory observations. Although three species of homalopsine snakes were encountered in the study areas (*Cerberus rynchops*, *Bitia hydroides*, and *Fordonia leucobalia*), *C. rynchops* was the most common species and is the subject of this report.

Initially, sampling along the shoreline at the primary site was conducted at all tidal stages and at sunrise, mid-morning, noon, mid-afternoon, sunset, and at night. Individuals of *C. rynchops* were observed during all tidal stages and times of day, but the snakes were most active on the surface of the mud flat, on the beach, and entering and leaving the stone wall from 1900–2200. During this time, snakes also were commonly on the leading edge of the incoming tide, and most of our collecting concentrated on this period. Notes on the time of capture, habitat, tidal stage, and water depth were recorded at the time of capture.

Following two to three hours of collecting, snakes were taken to our laboratory and palpated for stomach contents. If something in the stomach was detected by palpation but was not regurgitated,

then the snake was preserved and the contents were removed by dissection. The remaining snakes which failed to regurgitate any food were assumed to have empty stomachs (this assumption is supported by the dissection of a series of 24 snakes early in this work). Snout-vent length (sv) and tail length were then measured to the nearest 0.5 cm, and the snake was tagged (Floy Tag & Mfg. Inc., #FD-67C). Mass of the snake (Ms) was determined to the nearest gram by confining the snake with a plastic bag and placing it on a digital top-loading scale. The snakes were released within an hour of measurement at the shoreline in the center of the study area.

Prey items were immediately preserved using 10% formalin. After fixation, the maximum diameter and various lengths of the fish were measured to the nearest 0.1 mm, and after excess fluid was blotted off, the mass of the fish (Mf) was determined to the nearest 0.1 g. Based on preserved series of fish, linear least squares regressions estimated log Mf from the log of various measures of length from partially digested fish.

Three methods were used to estimate the proportion of diet comprised by each fish species. The occurrence of fish species was estimated as the percentage of stomachs in which they occurred as well as the percentage of the total number of items they comprised. The original wet biomass of each species was also estimated and then expressed as a percentage of the estimated total biomass of all prey consumed by one sample.

Observations were made on the feeding of freshly captured *C. rynchops* from 31 January–5 March 1984 and 10 December 1985–31 January 1986. Captive snakes were kept and observed feeding in 1.5 cm of fresh water inside white Styrofoam containers with an inside height, length, and width of 35, 40, and 60 cm, respectively. The snakes were observed feeding at times ranging from 1100–2300, with air temperatures ranging from 26°–32°C. Snakes that failed to feed at three consecutive trials were released. A total of 23 snakes (sv 29.5–60.0 cm) was observed feeding for 34 trials, during which 71 mudskippers (*Periophthalmus chrysospilos*) were consumed. The times between trials ranged from two to four days. For 19 trials involving 12 snakes, a single fish was offered to the snake. For the remaining trials, two to five fish were offered in rapid succession. No more than five feedings were observed per snake. Videotape facilitated the documentation of the 40 feedings during 1985–1986.

The total length (TL) of each fish was measured to the nearest millimeter immediately before of-

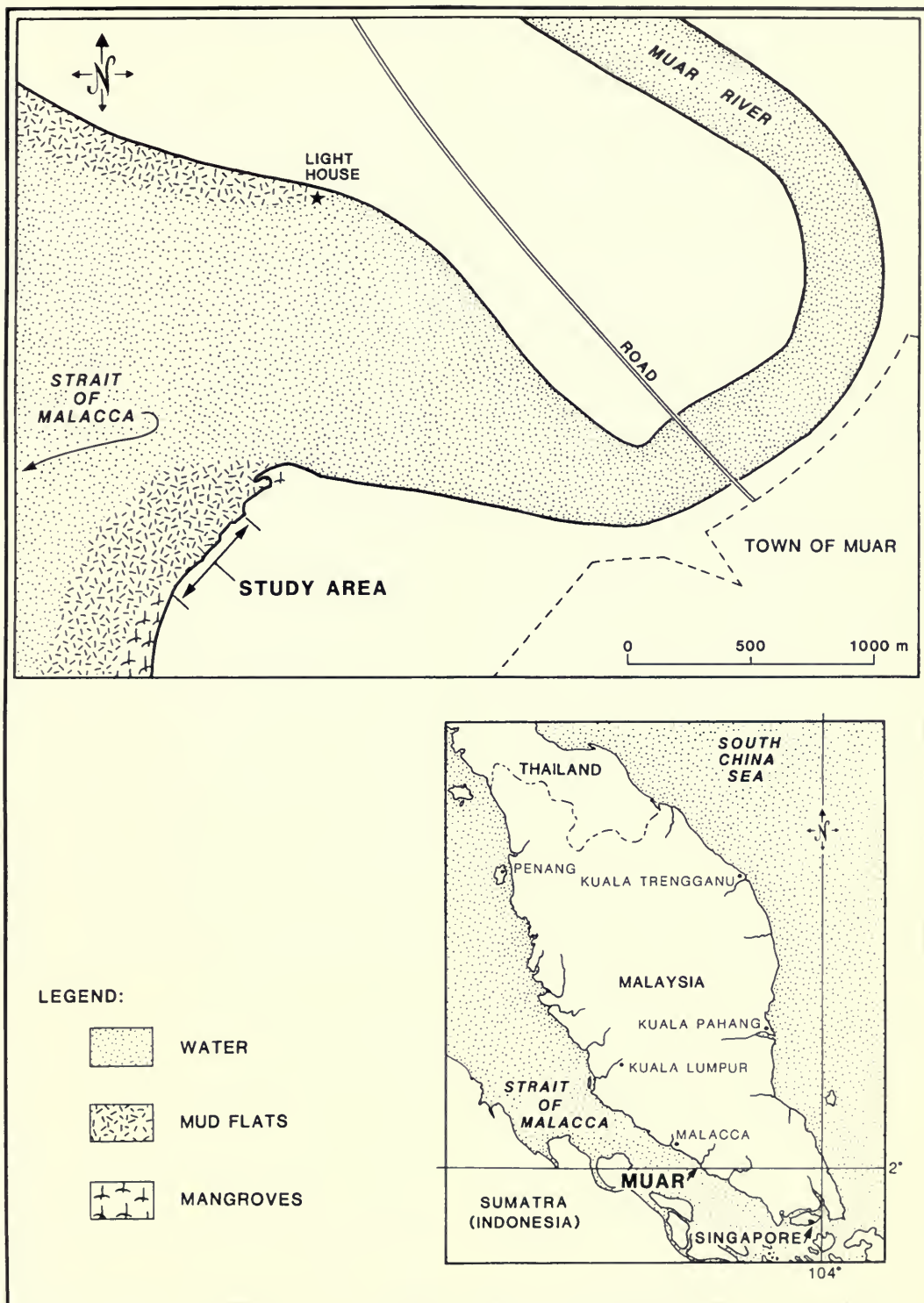


FIG. 1. Schematic map of the study site in the Muar estuary. Areas indicating mud flat estimate the extent of exposed mud during the spring low tides.

fering it to the snake. The TL ranged from 32–88 mm for the fish used in the experiments. The Mf were estimated to the nearest 0.1 g by a linear least squares regression ($\log[\text{Mf}] = 3.543[\log(\text{TL})] - 4.999$, $r^2 = .983$) which was calculated from the measurements of 24 fish that had been preserved in 10% formalin. For each trial, the initial position (IP) where the snake seized the fish was assigned a value from 1 to 4 as follows: 1 = the mouth of the fish was somewhere within the mouth of the snake, 2 = the snake bit the head or gill region while the mouth of the fish remained outside of the snake's mouth, 3 = the fish was seized between the posterior margin of the operculum and the posterior end of the first dorsal fin, and 4 = the fish was seized posterior to the first dorsal fin. The amount of struggle (s) by the fish after being seized was rated subjectively from 1 to 3 as follows: 1 = the fish only displayed slight movement when it was initially seized, 2 = the fish struggled slightly while it was being held, and 3 = the fish struggled more than twice and violently enough to substantially move the head and neck of the snake.

A digital stopwatch was used to determine (to the nearest second) the total prey handling time (Tt). Three phases were timed: holding time (Th), the initial seizure of the fish until the start of lateral jaw walking by the snake; jaw-walking time (Tjw), the start of lateral jaw walking until the snout of the fish was in the mouth of the snake; and swallowing time (Ts), the entrance of the snout of the fish into the mouth of the snake until the end of swallowing as indicated by the disappearance of the tail of the fish.

These various times of prey handling were analyzed as the dependent variable in three multiple regression models that were calculated using a hybrid stepwise procedure with an $F \geq 4.0$ ($P < .05$) as the criterion for addition or deletion from the model. Model 1 estimated Tt by summing separate regression estimates of Th, Tjw, and Ts. Occasionally, if a negative value was predicted for one of these three times, this estimate was changed to zero before adding it to the other times contributing to Tt. Models 2 and 3 each used a single multiple regression equation to predict Tt. Models 1 and 2 used a partial $F \geq 4.0$ ($P < .05$), whereas model 3 used partial $F = 2.9$ ($.05 < P < .10$) to determine the independent variables to be included in the multiple regression model. For all handling times sv, Ms, TL, Mf, IP, s, and ordinal number of fish within a trial were used as the independent variables. For Tjw and Ts, Th was also used as an independent variable.

Some *Cerberus rynchops* from Muar and Parit

Jawa were brought back to the United States for additional experiments. These snakes were maintained on a diet of live goldfish and were usually fed weekly in 1.5 cm of fresh water inside of a Plexiglas aquarium (75 cm long \times 50 cm wide \times 30 cm high). A 2-cm grid on white paper underneath the aquarium provided fixed points of reference.

Two experiments were conducted to clarify what stimulus might facilitate prey capture for *C. rynchops*. For both experiments the water temperature was from 28°–29°C, and the snakes were given five minutes to acclimate to the aquarium before being tested. In the first experiment, nine goldfish were placed in the aquarium for 30 minutes and then removed immediately prior to the introduction of a snake. At intervals of about 30 seconds, 0.5-ml samples of aquarium water were dropped into the aquarium from a hypodermic syringe held 30 cm above the water. The grid was used to estimate the distance between the head of the snake and landing point of the drops. The water was dropped only when all of the lower jaw of the snake was below the water's surface, allowing the drops to land laterally and anteriorly to the head of the snake. Four snakes were subjected to this stimulus ten times in succession, with two of the snakes receiving drops within 4–8 cm the first five times and 8–12 cm the second five times, and the other two snakes receiving drops in the reverse order. In the 2nd experiment, the same four snakes were subjected to a similar procedure with clean water in the aquarium. The aquarium was rinsed out ten times between trials. Results were only kept for snakes which ate a goldfish within five minutes of the conclusion of an experiment. Videotape recorded the orientation of the strike during some other regular feeding sessions with goldfish as prey.

Results

Diet

Of the 262 *Cerberus rynchops* collected and palpated in 1984, 97 had one or more prey items. In nine cases, however, the stomach contents were fed back to the snakes that had been captured for a second time; consequently, only the prey items of the remaining 88 snakes were analyzed. Of the 349 *C. rynchops* collected in 1985–1986, stomach contents were obtained from 93, and all of these items were retained for analysis.

A total of 313 items was removed from the 181

TABLE 1. Size distribution for samples of *Cerberus rynchops*.

Sample	n	Snake size classes by snout-vent length (cm)								
		25– 29.5	30– 34.5	35– 39.5	40– 44.5	45– 49.5	50– 54.5	55– 59.5	60– 64.5	65– 69.5
1984 diet	88	4.5	27.3	48.9	14.8	4.5
1985–1986 diet	93	1.1	15.0	22.5	18.3	17.2	11.8	5.4	5.4	3.2
15 Jan.–16 Feb. 1984	181	7.7	28.2	43.6	11.6	5.5	2.2	0.5	0.5	...
1–5 March 1984	67	3.0	20.9	41.8	23.9	5.9	4.5
20 Nov.–17 Dec. 1985	237	5.5	21.9	29.5	13.9	10.5	3.4	2.5	2.1	0.4
18 Jan.–8 Feb. 1986	112	5.4	17.0	19.6	16.1	12.5	17.0	4.5	7.1	0.9

Frequencies of occurrence are all given in percentages for each 5-cm size class within a sample.

The first two rows in the table indicate the snakes with prey items used for analysis of diet. The remaining rows indicate the size distribution of all snakes collected between the dates indicated at left.

n = Sample size.

C. rynchops with stomach contents. These snakes ranged from 26–67 cm in sv and from 19–208 g in Ms. The size distribution of snakes with stomach contents is summarized in Table 1. The stomachs of all these snakes mostly contained four species of oxydercine gobies, including 215 *Oxuderces dentatus*, 27 *Scartelaos pectinirostris*, 13 *Periophthalmus chrysopilus*, and 2 *Boleophthalmus boddarti*. Other gobiidae found in *C. rynchops* included six large, elongate fish (5 *Taeniodes cirratus* and 1 *Odontamblyopus rubicundus*) and two small fish of the genus *Acentrogobius*. Two species of catfish were represented by 19 specimens of Ariidae (*Arius* sp.) and one Plotosidae (*Plotosus* sp.). Twelve mullet (Mugilidae) were consumed, of which four were identifiable as *Liza* sp. and two as *Valamugil* sp. Two tongue fish (Cynoglossidae, *Cynoglossus* sp.) and two Sillaginidae (*Sillago* sp.) were also eaten. Only a single eel (Synbranchidae, *Macrotema* sp.) was removed from *C. rynchops*. One specimen each of Eleotrididae (*Butis* sp.) and Polynemidae (*Eleutheronema tetradactylum*) was also found. The remaining nine fish recovered from *C. rynchops* were not identifiable.

Of the 181 *C. rynchops*, slightly more than half (109) had only one item in the stomach. Of the remaining 72 snakes with multiple prey items, 38 had 2 items, 21 had 3 items, 5 had 4 items, 5 had 5 items, and 1 snake each had 6, 7, and 8 items; 25 of these snakes had taken only *Oxuderces dentatus*.

The size distribution of snakes with stomach contents collected in 1984 was significantly different from that of the 1985–1986 sample ($\chi^2 = 43.44$, $df = 8$, $P < .001$). Compared to snakes collected in 1985–1986, those sampled in 1984 had proportionately fewer individuals with sv > 45 cm (4.5% vs. 43%). To facilitate comparisons between snakes of the two study periods, an sv of

45 cm was used to subdivide samples. Table 2 summarizes the percentage of diet comprised by the major groups of prey species for small and large snakes. The 1984 and 1985–1986 samples of small snakes (sv < 45 cm) are very similar, with *Oxuderces dentatus* comprising the largest portion of diet using any of the three measures of importance. The diet of the large *C. rynchops* (sv > 45 cm) differs markedly from that of the smaller snakes. Although *O. dentatus* comprised the greatest portion of items in the larger snakes, it accounted for less than 10% of the biomass consumed. Equal percentages of large snakes contained *O. dentatus* and sea catfish, but the sea catfish had almost twice the biomass of the *O. dentatus*. Together, mullet and elongate gobies comprised less than 20% of the prey items; however, they accounted for nearly two-thirds of the prey biomass of the large snakes.

Predator/Prey Size Relationships

Total mass of the stomach contents per snake significantly increased with the Ms (fig. 2). These data were log transformed to equalize variance of the dependent variable. For the 181 snakes, log total mass of contents consumed per snake = $-1.198 + 0.875 \log Ms$; $r^2 = .24$. For example, this least squares regression predicts a 50-g snake would consume 1.94 g, about 4% of the Ms. These predicted masses of meals are much less than the maximum consumed by snakes. For example, one *Cerberus rynchops* (sv = 64 cm, Ms = 124 g) consumed a single mullet (*Liza* sp.; maximum height \times width = 37 \times 26 mm; Mf = 66 g) that was 53% of the Ms. However, meals of such large relative size were uncommon for the snakes sampled in this study. In fact, the second largest meal was another *Liza* sp., and it comprised only 28.8% of the Ms. Only 25 of the 181 snakes with contents

TABLE 2. Diet of *Cerberus rynchops*.

Sample	n	Percentage occurrence of prey species						
		Od	Sp	Pc	Ar	M	EG	Other
1984 <45 cm								
% Snakes	84	77.4	16.7	6.0	1.2	3.6	1.2	9.5
% Total items	155	79.4	9.0	3.2	0.6	1.2	0.6	1.2
% Prey biomass (total 131.9 g)	...	64.6	13.0	2.0	1.7	7.0	6.4	5.6
1985-1986 <45 cm								
% Snakes	53	67.9	17.0	9.4	9.4	3.8	0	15.1
% Total items	93	65.6	9.7	5.4	5.4	2.2	0	11.8
% Prey biomass (total 103.9 g)	...	52.9	8.1	7.4	8.9	1.4	0	21.2
1985-1986 >45 cm								
% Snakes	40	32.5	7.5	5.0	32.5	17.5	12.5	2.5
% Total items	58	43.1	5.2	5.2	22.4	12.1	8.6	3.4
% Prey biomass (total 271.5 g)	...	8.8	1.2	1.5	15.6	48.8	22.6	1.5

Od = *Oxuderces dentatus*; Sp = *Scortelaos pectinirostris*; Pc = *Periophthalmus chrysospilos*; Ar = ariid catfish; M = mullet; and EG = elongate gobies. See text for complete explanation of prey categories.

Percentage of snakes with prey species does not sum to 100 for a sample because of stomachs containing more than one species.

had relative mass of the total contents $\geq 10\%$. The snakes with the six largest relative masses of stomach contents each had consumed single fish, none of which were oxydercine gobies. The seventh largest set of contents consisted of three *Oxuderces dentatus* which were 18.4% of the mass of a 25-cm snake. Snake sv did not significantly affect the number of fish consumed ($F = .40$, $df = 1,179$; $P > .50$).

A detailed comparison of the size of the prey relative to the morphological limits of gape is beyond the scope of this study, but some evidence suggests that *C. rynchops* tends to take relatively small prey. Although the shape of fish may vary radically among different taxa, the maximum diameter of a fish approximates the difficulty a snake may have swallowing it. In addition to the mullet mentioned previously, some of the largest maximum diameters of fish consumed by *C. rynchops* were 13.0, 19.7, 19.9, and 31.7 mm for snakes with sv of 27, 38, 46, and 62 cm, respectively. In contrast to these large fish, 7.9 mm was the largest maximum diameter measured for any of the 216 *O. dentatus* consumed by *C. rynchops*.

Foraging

Water conditions at the Parit Jawa site often permitted observation of *Cerberus rynchops* foraging in water as deep as 1.3 m. Whether in water

or on mud flat, snakes were rarely sedentary for more than a minute. Swimming *C. rynchops* consistently moved along the bottom in contrast to the surface swimming that is commonly used by colubrid snakes such as *Nerodia* (Jayne, 1985). Snakes usually performed sidewinding locomotion on mud that was firm enough to support their weight. If snakes sank in mud past the first few dorsal scale rows, then lateral undulation was used for surface locomotion as well as swimming through the mud slightly below its surface. Snakes usually explored burrows and irregularities of the substrate regardless of whether they were under water. Occasionally, snakes swam with their mouths open slightly, and the lateral movements of the head were exaggerated compared to that during normal swimming. On two of these occasions, individuals of *C. rynchops* were observed capturing very small, schooling fish, and two other snakes used this behavior to capture an *Oxuderces dentatus* and a mullet that had just escaped after the snake attempted to swallow it. In two other instances, snakes swimming in muddy water were observed with this open-mouthed posture, but no fish could be seen. Another snake remained stationary, as it was in the midst of a school of fish, and it repeatedly used similar alternating lateral movements of the head and neck until the school of fish dissipated. Two other strikes at fish observed in the field also seemed to have a distinct lateral component.

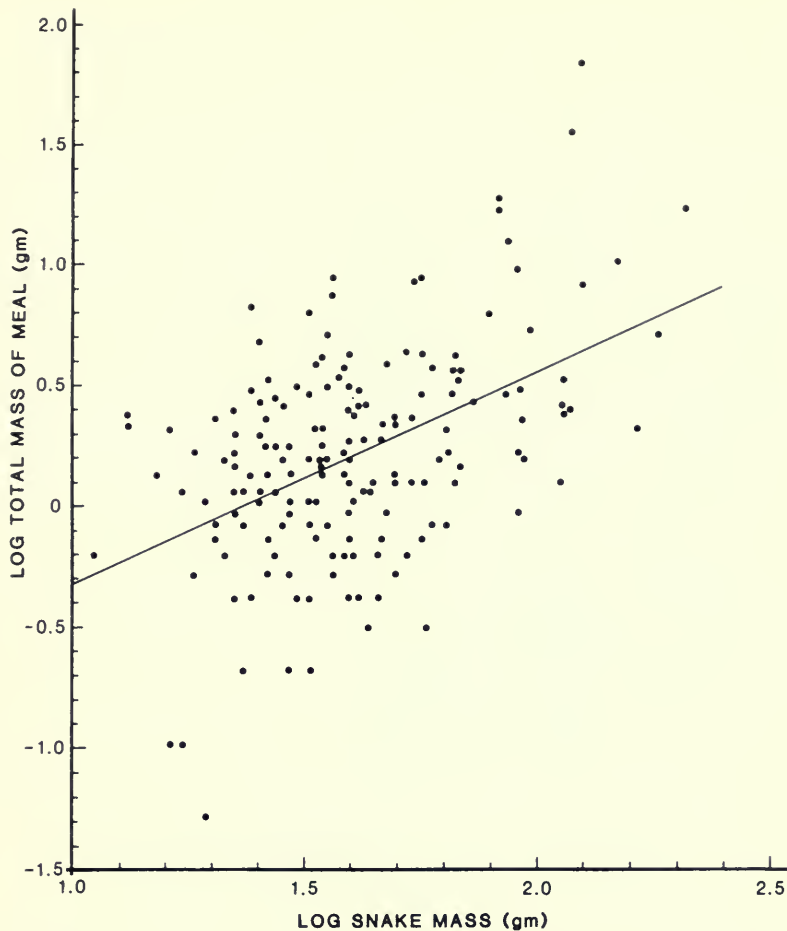


FIG. 2. Plot of log total mass of stomach contents versus log mass of snake for the 181 *Cerberus rynchops* with prey items. Both masses were originally in grams. The line indicates the least squares regression, where log mass of stomach contents = $-1.198 + 0.875 \log \text{ snake mass}$, $r^2 = .24$.

Analysis of video tapes of 65 strikes of captive-fed *C. rynchops* confirmed that there was always a lateral movement involved in aquatic prey seizure (fig. 3). The initial phase of the strike could be directed in nearly any direction; however, a subsequent rapid lateral flexion of the neck momentarily caused a posture with the anterior region of the snake forming an arc of about 270° (fig. 3). This quick lateral flexion usually occurred just as the snake's mouth contacted the fish. During this stage of prey seizure, the fish would often not be grasped securely in the snake's jaws, and the orientation of the snake frequently trapped the fish between the snake's mouth and body. This enabled some snakes to quickly reposition their jaws or to recapture fish that had momentarily escaped.

Feeding Behavior

The following descriptions are representative of the variation in observed captive feeding behavior. The figures in parentheses indicate the elapsed time (in seconds) after the snake initially seized the fish.

A *Cerberus rynchops* (sv = 32 cm, Ms = 22 g) seized a *Periophthalmus chrysospilos* (TL = 75 mm, Mf = 4.7 g) just posterior to the operculum as the fish was moving near the snake. Immediately after striking the fish, the snake rapidly moved the fish back to the corners of its mouth and held the fish perpendicular to its neck. During this initial seizure, the fish moved only slightly. As the snake continued to hold the fish, there were occasional

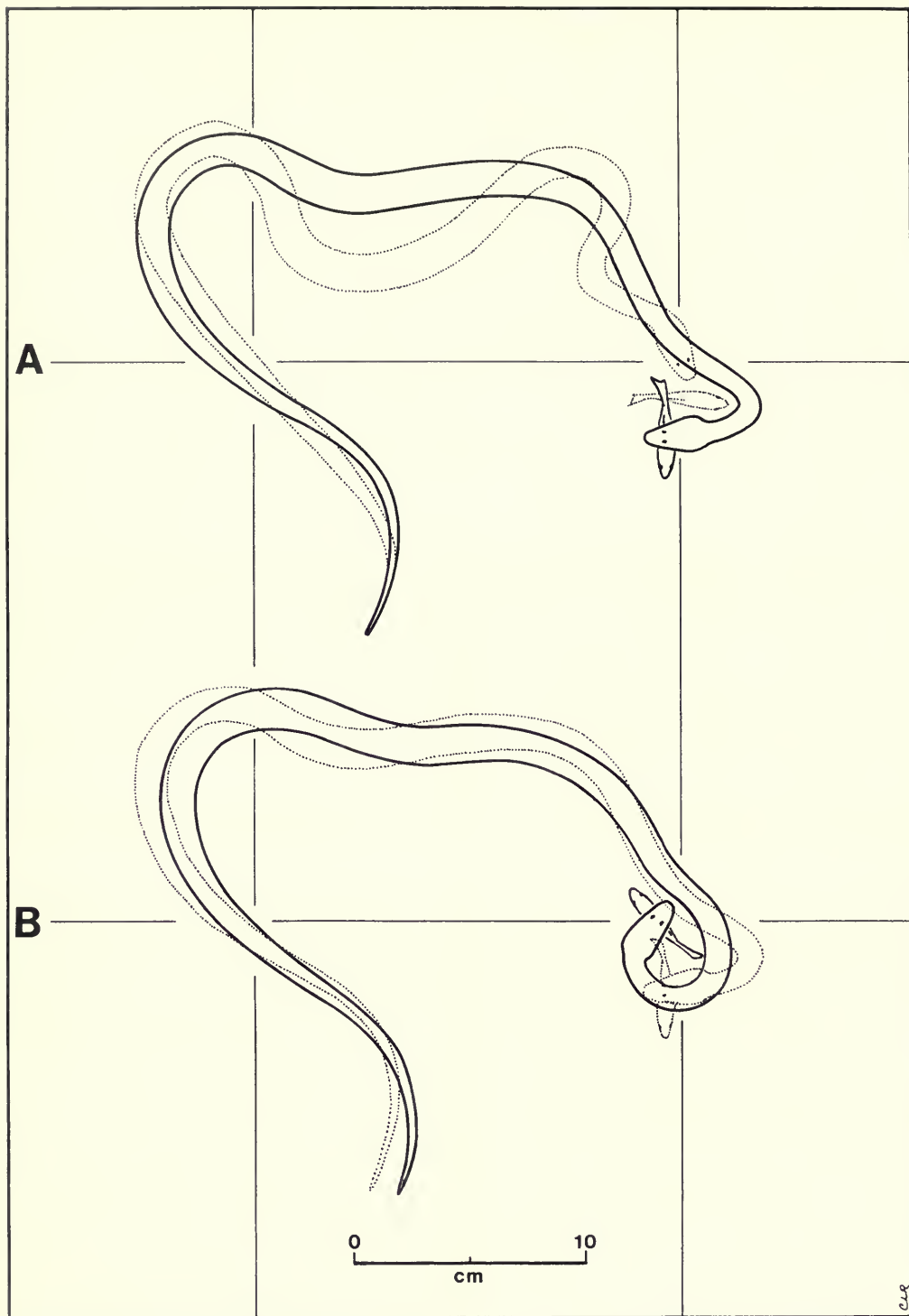


FIG. 3. Striking behavior of *Cerberus rynchops* attacking a goldfish. The illustration is based on tracings made from videotape. Pairs of successive images are superimposed, with the dotted outline indicating the earlier position in each pair. A, Position at time = 0 and 1/15 second; B, position at time = 1/15 and 2/15 second.

TABLE 3. Coefficients for multiple regression equations predicting prey handling times for *Cerberus rynchops* consuming *Periophthalmus chrysospilos*.

Dependent variable (sec)	Coefficients of independent variables				Constant (sec)	Multiple r^2
	Mf (sec/g)	SV (sec/cm)	S (sec)	IP (sec)		
Model 1						
Th	62.1 (.37)	-7.79 (-.28)	105 (.31)	NS	117	.43
Tjw	12.4 (.52)	-1.13 (-.29)	NS	9.29 (.31)	18	.50
Ts	11.3 (.45)	-1.78 (-.43)	NS	NS	79	.35
Model 2						
Tt	84.1 (.43)	-10.1 (-.32)	125 (.32)	NS	185	.53
Model 3						
Tt	83.0 (.43)	-10.7 (-.34)	94 (.24)	39* (.16)	166	.55

Figures in parentheses after coefficients are standardized regression coefficients.
n = 71 for all regressions; NS = not significant; sv = snout-vent length of snake; Mf = mass of fish; IP = initial position where snake seized fish; and s = struggle of fish.
*Partial $F = 2.95$ ($.05 < P < .10$).

biting-like movements of the snake's maxillae (20, 278, and 392). While the fish was being held by the snake, some fin, gill, and mouth movements were apparent. The snake then began to lateral jaw walk toward the snout of the fish (400) while the fish showed only very slight gill and mouth movements. Immediately after reaching the snout of the fish (507), swallowing began and continued until the tail of the fish disappeared from view (590). As the snake was swallowing, no fish movements could be discerned.

The duration of this holding behavior by *C. rynchops* varied considerably as illustrated by another individual (sv = 36.5 cm, Ms = 35 g) that ate a mudskipper (TL = 69 mm, Mf = 3.5 g). This snake seized the fish on the gill region, and the fish flopped violently as the snake briefly held it. The snake started slow lateral jaw walking to the snout of the fish (9) as the fish continued to make whole body undulations. Upon reaching the snout of the fish (63), the snake started swallowing, and the fish continued to move slightly until its tail disappeared from view (94).

During another trial, a snake (sv = 34 cm) was disturbed and released the fish (2.5-g mudskipper) after holding it for 117 seconds. The snake was then removed from the container, and the fish was observed until it died 16.5 minutes after being seized. During other feeding trials with mudskippers, as the snake held the fish, there was sometimes a marked darkening of the fish that spread from the site of the bite. Occasionally, there was also a noticeable dilation of the pupils of the mudskippers while they were being held. In the field, a *C. rynchops* was observed holding a mullet (TL

= 82 mm, Mf = 7.2 g) that was still moving slightly. By the time the snake was captured, the fish had been released and had died. In the laboratory, several snakes (sv = 29–51 cm) were forced to release goldfish (0.8–3.7 g) just as lateral jaw walking began. The Th varied from 0.2–6.9 minutes. Of the 31 observed goldfish, 16 died after being held from 1.1–6.9 minutes. The times of death after initial seizure ranged from 6.0–44.0 minutes; nine of these 16 goldfish died in less than 16.5 minutes after being seized by snakes. Hence, the venom of *C. rynchops* appears capable of immobilizing and killing selected prey.

Table 3 summarizes the coefficients of the significant independent variables in the various multiple regression equations. As suggested by the standardized regression coefficients, the Mf was always the most significant factor affecting all prey handling times. Increased sv of the snake always significantly decreased handling times. Struggling by the fish primarily increased Th. More posterior IP increased predicted Tjw. Interestingly, Th (and presumed envenomation) did not significantly affect Tjw or Ts.

Table 4 lists select predicted values for the three models of total handling time. The Ms can be predicted from sv by the least squares regression $\log Ms = 2.878(\log sv) - 3.018$, $r = .969$, $n = 181$. A 45-cm *C. rynchops* has about twice the mass of a 35-cm snake (55 vs. 27 g). For a given size, s, and IP of mudskipper, predicted Tt for the 45-cm snake can be from $\frac{1}{3}$ – $\frac{2}{3}$ that predicted for the 35-cm snake. For a given snake, handling a 2-g mudskipper may take from $\frac{1}{2}$ – $\frac{1}{3}$ the Tt predicted for a 4-g fish. Increased struggle of the fish may cause

TABLE 4. Predicted handling times (in seconds) for *Cerberus rynchops* eating *Periophthalmus chrysospilos* (see text for explanation of models).

Independent variable				Model 1				Model 2	Model 3
Mf (g)	sv (cm)	s	IP	Th	Tjw	Ts	Tt	Tt	Tt
2	35	1	3	74	31	39	144	124	169
4	35	1	3	198	54	62	314	208	252
2	35	1	2	74	21	39	134	208	213
4	35	1	2	198	47	62	307	292	379
4	45	1	3	119	44	44	198	191	247
4	45	1	2	119	35	44	189	191	208
2	45	1	3	0*	19	21	40	23	42
2	35	3	3	284	30	39	353	374	238
2	45	3	3	206	19	21	246	273	240
2	45	1	1	0*	1	21	22	23	-182
4	55	1	3	42	33	26	101	91	120
4	55	3	3	252	33	26	311	340	318
2	55	1	3	0*	9	4	13	-78	-36

* Negative value was changed to 0.

Mf = Mass of fish; sv = snout-vent length of snake; s = struggle of fish; and IP = initial position where snake seized fish.

up to a sixfold increase in Tt and elicit holding behavior as well.

The data from the stimulus experiments were tallied as strike or no response, combined for all four of the snakes ($n = 40$), and arranged into two-by-two contingency tables for chi-squared analysis ($\chi^2 = 3.84$, $P < .05$ used for decision-making). For the experiment using water with fish odor, 10 of the 16 strikes occurred during the first half of each trial using clean water. Hence, for water with fish odor ($\chi^2 = 1.67$) and for clean water ($\chi^2 = 0$), response does not appear to be dependent on the number of stimuli within each trial. In other words, the snakes did not appear to be habituating to the ten stimuli within each trial. When using the water with fish odor, 15 strikes resulted from stimulus within 4–8 cm of the head of the snake, and only one strike occurred for the 8–12-cm distance; therefore, response was dependent on the distance from the stimulus ($\chi^2 = 20.67$). For the experiment with clean water, 12 strikes were within 4–8 cm, and six strikes were within 8–12 cm. The χ^2 was equal to 3.64, just slightly less than the critical value. During all of the experiments and routine feeding sessions, on only two occasions did snakes attempt to strike at a handler or at moving objects above the surface of the water. Thus, the response to the waterdrop stimulus does not appear to be defensive or visual in nature. Instead, this response appears to be predatory and largely the result of tactile stimulus.

Growth

As indicated by a high incidence of zero and negative growth of 35 snakes recaptured in 1984 less than 20 days after marking, short-term growth was probably obscured by measurement error and handling stress. Consequently, the samples analyzed here are confined to 24 snakes recaptured after 20 or more days. Table 5 lists relative growth

TABLE 5. Snout-vent lengths and masses for 14 of the 24 recaptured *Cerberus rynchops* with the greatest percentage increase in mass.

Snake no.	Elapsed days	Initial sv (cm)	Initial Ms (g)
628	20	32.5 (1.5%)	19 (15.8%)
630	20	38.0 (3.9%)	35 (28.6%)
3103	25	43.0 (1.2%)	50 (14.0%)
3090	26	30.5 (1.6%)	16 (18.8%)
3073	27	38.0 (1.3%)	29 (20.7%)
3074	28	37.0 (2.7%)	28 (14.3%)
3094	28	42.0 (1.2%)	42 (21.4%)
3045	28	49.0 (2.0%)	70 (17.1%)
630	29	38.0 (3.9%)	35 (17.1%)
3023	32	40.0 (8.8%)	41 (17.1%)
1091*	42	40.5 (6.0%)	39 (25.6%)
1030*	45	50.0 (2.0%)	67 (23.9%)
1038*	65	44.5 (3.8%)	51 (13.7%)
922*	68	60.0 (5.0%)	124 (8.1%)

Figures in parentheses indicate percentage increase between initial and final capture.

* Captured during 1986.

for some of these snakes with the greatest increase in Ms. At initial capture, the sv of the 1984 sample of 15 snakes ranged from 30.5–49.0 cm (\bar{x} = 38.5 cm, s = 5.04), and the Ms, from 16–70 g (\bar{x} = 36.67 g, s = 15.31). The average elapsed time between captures for this group was 26.7 days. Growth varied considerably; on average, these snakes gained mass at 0.50%/day (range –0.19%–0.76%/day, s = 0.40) and grew in sv at 0.11%/day (range 0%–0.19%/day, s = 0.075). The nine snakes recaptured in 1986 initially ranged from 40.5–60.0 cm sv (\bar{x} = 49.3 cm, s = 19.3) and from 32–124 g (\bar{x} = 54.4 g, s = 28.1). Average time between captures was 44.8 days (s = 6.5) for this group. Average growth rates for the 1986 recaptures were 0.12%/day (range –0.28%–0.61%/day, s = 0.151) for Ms and 0.06%/day (range 0%–0.27%/day, s = 0.04) for sv. For both samples combined, average growth rates were 0.36%/day (s = 0.40) for Ms and 0.09%/day (s = 0.07) for sv.

Population Structure

Table 4 lists the distributions of snake sv for two subsamples each for 1984 and 1985–1986. Using a chi-square test, no significant differences were found between the two subsamples within 1984 (χ^2 = 11.47, df = 7, $.1 < P < .2$). Similarly, no differences in size distribution were evident when comparing the 1985 to the 1986 subsamples (χ^2 = 13.30, df = 9, $.1 < P < .2$). This and the fact that small snakes (sv < 30 cm) were continuously encountered during this study suggest that reproduction of this population is aseasonal. When the total size distribution of 1984 was compared to that of 1985–1986, a highly significant difference was found (χ^2 = 77.18, df = 9, $P \ll .001$).

Population Size Estimates

Although most collecting was confined to habitats within the primary study site, two adjacent habitats were investigated. On the landward side of the beach and stone wall, there was a mowed soccer field and an unmowed grass field with a large freshwater pond. No *Cerberus rynchops* were observed in about six man-hours of exploring and traversing this area. The portion of the river mouth below the low tide level and about 100 m north of the east end of the study site is serviced by two stake nets. These nets have produced extensive collections of sea snakes since 1975 (Voriss et al.,

1978; Voriss & Jayne, 1979; Voriss, 1985), but rarely trapped *C. rynchops*. These observations and the high concentrations of subadults encountered in the study area lead us to believe that we could estimate the subadult population in the study area within a limited period of time.

Three estimates were made. For the first estimate, 108 snakes were marked and released between 15 January and 10 February 1984. Collecting on 12–13 February produced 32 unmarked snakes and 12 previously marked snakes. Using Bailey's (1952) formula the population size estimate is 374 (s = 84.3). For the second estimate, the snakes collected on 12–13 February and two other snakes collected earlier were marked and released. The population was not disturbed by us from 15 February–1 March. From 1–5 March, we collected 44 unmarked snakes and 21 marked previous to 15 February. Bailey's estimate for these data is 426 (s = 72.5). In 1985–1986 the third estimate was made. From 20 November–17 December 1985, 210 snakes were marked. The snakes were left undisturbed until 18 January–8 February 1986, whereupon 112 animals were collected. Of the 16 recaptures during this period, seven had Floy tags, and the rest had conspicuous scars where the tags had pulled out. Bailey's estimate for this period was 1,396 (s = 303).

During the strongest tides, the area of the intertidal zone within the study site is about 80,000 m². The conspicuous concentration of snakes at the edge of the water and the unknown extent to which deeper water is utilized by the snakes, however, complicate calculation of the density per unit area attained by *C. rynchops* at this site. Nevertheless, these estimates of population size suggest there may be from one to three subadult snakes per meter of shoreline within the primary study site.

Discussion

For the communities of marine snakes that have been previously studied, little or no overlap in diet has been found. For a community of ten hydrophiids on the Ashmore reef in Australia, McCosker (1975) found practically no overlap in either the diet or microhabitat preferences of the different species. Similarly, for four different communities of acrochordids and hydrophiids in Malaysia, Voriss and Voriss (1983) found most species were dietary specialists, and only modest overlap occurred

among the more dominant species of the community. *Lapemis hardwickii* is a notable exception to this trend, as this hydrophiid has a very generalized diet (Voris & Voris, 1983).

In the Muar estuary, the homalopsine *Fordonia leucobalia* feeds exclusively on crabs and has no dietary overlap with other snakes. Preliminary analysis of the diet of *Bitia hydroides* suggests this homalopsine feeds primarily on gobies and hence has overlap with the diet of *Cerberus rynchops*. *Acrochordus granulatus* captured from the Straits of Malacca consume about 46% Eleotrididae and 54% Gobiodei with taenioid gobies comprising 7.7% of the prey items (Glodek & Voris, 1982).

The diets of juvenile and adult *Enhydrina schistosa* are comparable, and this species, which is the most abundant hydrophiid at Muar, consumes 76.7% ariid and 13.8% plotosid catfish (Voris et al., 1978). The second most abundant hydrophiid at Muar (*Hydrophis melanosoma*) eats exclusively eels (Glodek & Voris, 1982). Various gobies comprise about 10% of the prey items of the third most abundant hydrophiid (*Hydrophis brookii*) at Muar. *Hydrophis torquatus* is the only other hydrophiid at Muar for which dietary information is available, and small samples suggest this species consumes 60% taenioid gobies (Glodek & Voris, 1982).

The extent of diet overlap can be calculated using the Schoener (1968) index, α . For the 1985–1986 sample of large *C. rynchops* compared with *Enhydrina schistosa*, $\alpha = .17$, whereas overlap between *E. schistosa* and 1985–1986 small *C. rynchops* was only .05. Using the species level for grouping prey items, no overlap occurred between *C. rynchops* and either *H. melanosoma* or *H. brooki*. For large *C. rynchops* compared with *H. torquatus* and *A. granulatus*, $\alpha = .07$. For the more abundant snake species within a community, Glodek and Voris (1982) found α rarely exceeded .10.

The extent to which dietary overlap is determined by predator choice versus microhabitat preferences remains unclear. During all of the collecting of homalopsines at Muar and Parit Jawa, not a single hydrophiid was seen. The extensive use of fishing nets has captured hundreds of hydrophiids in the main channel of the Muar River (Voris et al., 1978); however, these same nets have yielded less than ten homalopsines. The relative scarcity of adult *C. rynchops* collected from the tidal edge and the occurrence of prey such as *Taeniodes cirratus* imply that large individuals of *C. rynchops* are more likely to occur in deeper water than small individuals. Unfortunately, it is difficult to collect snakes in this most probable region

of interspecific spatial overlap at water depths ranging from 1–3 m. Yet it seems likely that the greater dietary overlap of *E. schistosa* and large *C. rynchops* is primarily the result of ontogenetic changes in habitat preference which cause the relatively opportunistic *C. rynchops* to overlap more with the more specialized diet of *E. schistosa*.

Feeding Behavior

Aspects of the feeding behavior of *Cerberus rynchops*, such as prey detection, capture, and handling, resemble those of other aquatic snakes. *Cerberus rynchops* used a predominately lateral strike to capture prey. *Pelamis platurus* is a surface feeding hydrophiid, and it also uses a lateral strike to capture fish (Pickwell, 1972; Kropach, 1975). Another hydrophiid, *Enhydrina schistosa*, feeds primarily along the bottom and it also uses a lateral strike to capture fish. Both *P. platurus* and *E. schistosa* hold and envenomate fish and wait until struggling ceases before swallowing (Pickwell, 1972; Voris et al., 1978). As shown in this study, *C. rynchops* were more likely to hold (and presumably envenomate) fish that were relatively large or struggled vigorously. However, initiation of swallowing by *C. rynchops* may or may not occur before the fish has stopped struggling. Despite the sharp spines present in the dorsal and pectoral fins of ariid catfish, some individuals of *C. rynchops* in the field were observed swallowing these catfish while they were still moving. Catfish are always consumed head first by *E. schistosa* (Voris et al., 1978) and by individuals of *C. rynchops* observed in this study. As one might expect for snakes that inhabit muddy water and have nocturnal tendencies, *C. rynchops* readily showed striking behavior when exposed to mechanical stimulus. Feeding of *P. platurus* also appears responsive to mechanical stimulus (Kropach, 1975). As evidenced by the ability of *E. schistosa* to feed in total darkness, some combination of tactile and olfactory cues appear sufficient for prey capture and consumption (Voris et al., 1978).

In a series of carefully controlled experiments, Drummond (1979, 1985) has examined the effects of visual and olfactory stimuli on predatory behavior of certain piscivorous natricine snakes. Drummond (1979) found that individuals of *Nerodia sipedon* were not entirely dependent on chemical cues to locate and capture fish. Moving models of fish were more effective than nonmoving models for eliciting orientation, attacking, and searching

behavior by *N. sipedon*. Among the predatory behaviors described for *N. sipedon*, Drummond (1979) found that open-mouthed searching (i.e., lateral sweeps with open jaws usually while the snake was moving) was used when *N. sipedon* were under water, and this behavior did not require visual stimulus, being more likely to occur after an unsuccessful attack. These observations of open-mouthed searching correspond closely with those for a *C. rynchops* which was seen behaving in this fashion at night, in muddy water, and after an unsuccessful attack.

Drummond (1985) isolated visual and mechanical stimuli for predatory behavior of natricines and found that, in the presence of diffuse fish odor, visual stimulus could elicit an attack. The role of visual stimulus for predation by *C. rynchops* remains unclear. Compared to *N. sipedon*, the eyes of *C. rynchops* appear substantially smaller. The *C. rynchops* that were fed *Periophthalmus* in Malaysia only attacked fish that were moving, but mechanical and chemical stimuli were also present in these trials. *Cerberus rynchops* that were maintained in the United States for a longer duration would attack nonmoving fish. During the daytime, some attempts were made to capture *C. rynchops* by reaching down from the seawall. The *C. rynchops* were very adept at evading this method of capture, and they usually dove below the surface of the water even before the hand entered the water. Hence, it is clear that *C. rynchops* can respond to visual stimulus within about 1 m. Yet, the fact that *C. rynchops* would attack vibrations caused by waterdrops suggests visual stimulus may be minimally important for the predatory behavior of this species. Future, more controlled studies comparing homalopsines, natricines, and hydrophiids should clarify different roles of various stimuli on their predatory behavior.

Growth

The average growth rate of 0.165 g/day for this small sample of *C. rynchops* is about one-third the estimated rate of 0.49 g/day for the sea snake *Enhydrina schistosa* in this same estuary (Voris, 1985). The growth in sv of 0.42 mm/day for this sample is also substantially less than the 1.0 mm/day estimated for *E. schistosa* in the first year of life (Voris & Jayne, 1979). One potential factor affecting growth rate is the amount of prey consumed. The total estimated biomass of prey taken by *C. rynchops* was 514.2 g, which was 6.21% of

the total biomass (8,282 g) of the snakes that consumed them. Only 29.6% of the *C. rynchops* examined had stomach contents. Assuming the sample of snakes with stomach contents was a random subsample of all the snakes collected, one can estimate the biomass (in grams) of all the examined snakes by the formula: $8,282 \times (100/29.6) = 27,979$. Hence, the corrected ratio of biomass of prey consumed to biomass of predator equals 1.84%. Similar estimates of these ratios can be calculated for the data set of 104 catfish (Voris & Moffet, 1981) consumed by *E. schistosa* at Muar. *Enhydrina schistosa* consumed an estimated 1,174 g of fish which was 9.27% of their total biomass of 12,672 g. However, only 19.6% of the *E. schistosa* had stomach contents. After correcting for percentage of stomach contents, the ratio of total prey biomass/predator biomass becomes 1.81% for *E. schistosa*, and this figure is remarkably similar to that of *C. rynchops*.

These gross estimates of prey consumption ignore the cost of capturing prey. *Cerberus rynchops* was often sighted actively foraging, and on the average it was taking relatively more and smaller prey items than *E. schistosa*. Thus, *C. rynchops* may be a more active forager than *E. schistosa*.

Reproduction and Population Numbers

The lack of a comprehensive collection prohibits definitive conclusions about the reproductive cycle of *Cerberus rynchops* at Muar. Snakes were only preserved sporadically when stomach contents were not regurgitated. Two gravid females with barely visible embryos were collected 2–4 December 1985. One female (sv = 67 cm, Ms without embryos = 208 g) contained 27 embryos, and the combined mass of these eggs was 39 g. The other snake (sv = 55 cm, Ms = 127 g) contained 12 embryos which totaled 20 g. From 1–8 February 1986, three large females were preserved. Two of them (sv = 62.5, 64 cm) had neither embryos nor enlarged follicles. The third female (sv = 62 cm, Ms = 163 g) contained 18 very early embryos weighing 29 g. Hence, the condition of these reproductive tracts further supports a supposition of no strong seasonality of reproduction for the *C. rynchops* at Muar.

In contrast to the population at Muar, Saint Girons (1972) suggested that the reproductive cycle of *C. rynchops* in Cambodia conformed to that of other Cambodian homalopsine species. These homalopsines generally start vitellogenesis in No-

vember, mating probably occurs in December to early January, and parturition occurs in May (Saint Girons, 1972). For *C. rynchops* in Java, Bergman (1955) found females with eggs in the oviducts in March, April, May, July, and October; however, some months were not sampled. Smith (1943) reported sv of newborn snakes ranging from 17.5–20.0 cm and brood size ranging from 8 to 26. Considering this size of newborn snakes and the continual occurrence of snakes between 25 and 30 cm, it is puzzling that no snakes shorter than 25 cm were collected. Perhaps births were occurring in a different habitat, or there is some very weak seasonality of reproduction.

Enhydrina schistosa, the most common hyrophiid occurring in the Muar estuary, shows marked seasonality in reproduction. Voris and Jayne (1979) found that vitellogenesis in this species occurs during November to December, ovulation probably occurs in December, and young are born from mid-February through March. *Hydrophis melanotosoma*, *H. brookii*, and *H. torquatus* are the next most common hydrophiids at Muar, and their reproductive cycle is similar to that of *E. schistosa* (Lemen & Voris, 1981). Limited data are available for the reproductive cycle of *Acrochordus granulatus* at Muar. However, collections of *A. granulatus* from two sites on the west coast of Malaysia, one within about 241 km of Muar and the other 80 km from Muar, suggest this species is aseasonally reproductive (Voris & Glodek, 1980).

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